Journal of Mammalogy, 88(1):241–249, 2007

RODENT COMMUNITIES IN ACTIVE AND INACTIVE COLONIES OF BLACK-TAILED PRAIRIE DOGS IN SHORTGRASS STEPPE

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Black-tailed prairie dogs (*Cynomys ludovicianus*) alter shortgrass-steppe landscapes in ways that are expected to affect other mammals. I sampled rodent populations at 31 sites on the Pawnee National Grasslands, Colorado, including 18 active colonies, 6 colonies that had been unoccupied for >6 years (inactive), and 7 grassland sites without prairie dogs (controls). Rodents were livetrapped for 4 consecutive nights at each site between May and August 2004 to estimate relative abundance. I also measured vegetation and habitat characteristics. Northern grasshopper mice (*Onychomys leucogaster*) and 13-lined ground squirrels (*Spermophilus tridecemlineatus*) were captured on most (≥87%) of the sites and comprised 40% and 34% of individuals captured, respectively. Species richness ranged from 1 to 6 species, but most sites had only these 2 species. Grasshopper mice tended to be more abundant on colony sites than on controls, although differences were not statistically significant. Ground squirrels were least abundant on active colonies, and most abundant on inactive colonies, followed by controls. Habitat types did not differ in their abundance of any other species or in total rodent abundance; however, active colony area influenced total rodent abundance, with small colonies supporting fewer individuals. Controls supported the most rodent species, in part because these sites consistently had taller grass, which presumably provided habitat and food for less common species (*Chaetodipus hispidus*, *Perognathus flavus*, and *Reithrodontomys megalotis*). In shortgrass steppe, active colonies provided habitat for grasshopper mice, which may be involved in maintenance and spread of plague, but did not support consistently higher rodent species richness than the surrounding grasslands.

Key words: *Cynomys ludovicianus*, grassland biodiversity, habitat associations, *Onychomys leucogaster*, *Peromyscus maniculatus*, PRIMER, rodent communities, shortgrass prairie, *Spermophilus tridecemlineatus*

The grazing and burrowing activities of prairie dogs significantly alter grassland landscapes, creating and modifying habitat for other species, including other small mammals (Kotliar et al. 1999; Stapp 1998). Comparative studies of the ecological effects of prairie dogs on grassland biodiversity have suggested that some small mammals benefit from the presence of prairie dogs, whereas others are negatively affected or show little response (Agnew et al. 1986; Ceballos et al. 1999; Davidson et al. 1999; Lomolino and Smith 2003; O'Meilia et al. 1982). In many cases, these contrasting results may be explained by differences in types of grassland studied and the effect of the intensive grazing and mound-building in colonies relative to the surrounding vegetation (Stapp 1998). Studies conducted in the mixed-grass prairies, for example, suggest that the short vegetation of colonies represents relatively unique habitat that may enhance rodent diversity at the landscape scale, whereas the few studies undertaken in shortgrass prairie are more equivocal.

Recent concern about the historical, anthropogenic declines of prairie dogs across their range prompted efforts to list the black-tailed prairie dog (*Cynomys ludovicianus*) as Threatened under the Endangered Species Act (Miller and Cully 2001). Although the petition was ultimately rejected in 2004, the United States Fish and Wildlife Service concluded that the most significant threat to the persistence and recovery of the species was sylvatic plague, a disease caused by the bacterium *Yersinia pestis* that was introduced to North America in about 1900 (Barnes 1993; Cully and Williams 2001). Prairie dogs are extremely vulnerable to plague mortality, and the extinction of entire colonies after epizootics may have significant effects on the persistence of prairie dog metapopulations (Stapp et al. 2004), as well as the small rodents and other vertebrates commonly found in colonies. Small rodents may also play a role in the dynamics of plague; some species, such as the deer mouse (*Peromyscus maniculatus*) and northern grasshopper mouse (*Onychomys leucogaster*), show limited resistance to

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plague and have been suggested to act as reservoirs for the bacterium or flea vectors (Davis et al. 2002; Marchette et al. 1962; Thomas et al. 1988), increasing spread during outbreaks and allowing the bacterium to persist after prairie dogs have succumbed to disease. Other species, such as the 13-lined ground squirrel (*Spermophilus tridecemlineatus*), have been suggested to be susceptible to the disease (Cully et al. 1997) and may amplify its spread during outbreaks.

As part of a broader study of the ecology of plague in small mammals and prairie dogs in shortgrass steppe in north-central Colorado, I compared rodent communities associated with active and inactive colonies and comparable grassland areas lacking prairie dogs. Here, I address 2 questions. First, what small rodents are associated with prairie dog colonies and with the surrounding grasslands? Second, are there differences in habitat characteristics among colonies and grassland areas that might explain patterns of rodent abundance? My sampling approach was primarily extensive, in that I chose to survey a large number of colonies of different activity levels, rather than studying a few sites intensively over time. I chose this approach to try to sample as much of the local spatial variability among colonies as possible, and to identify how relative abundance and species composition might be influenced by colony activity. Knowledge of the patterns of abundance and diversity of rodents associated with shortgrass-steppe colonies may provide clues as to the involvement of these species in plague epizootics.

Materials and Methods

The study area was the Pawnee National Grasslands (PNG), located approximately 40 km northeast of Greeley in Weld County, Colorado. The PNG consists of 78,129 ha of mixed federal, state, and private lands and is administered by the United States Department of Agriculture Forest Service. The climate is semiarid, with cold, dry winters; most of the 322 mm of annual precipitation falls as rain between April and September (Lauenroth and Milchunas 1991). The vegetation is classified as shortgrass prairie, and is dominated by 2 perennial warm-season grasses (*Bouteloua gracilis* and *Buchloe dactyloides*). Cattle grazing is the primary agricultural use on federal lands, with grazing and winter-wheat and forage crop (alfalfa and corn) production on private lands. In 2003, the number (27) and active area (857 ha total or 1.1% of PNG; mean area = 32 ha) of black-tailed prairie dog colonies on the PNG were the highest since regular monitoring began in 1981. Over the 23-year period, an average of 19 colonies, covering a total of 262 ha, were active each year, with the fewest number of colonies (9) and smallest active area (74 ha; 0.1%) recorded in 1983 (Stapp et al. 2004).

In 2004, small mammals were livetrapped on 31 PNG sites representing 3 different habitat types. Eighteen sites were on active prairie dog colonies (hereafter, active), which ranged in area from 0.8 to 175.7 ha in 2003. The area of each active colony is estimated each year by the United States Forest Service biologists in early fall by walking or driving the perimeter of each colony and mapping locations of active burrows using a global positioning system unit (Stapp et al. 2004). Six sites were on colonies that had been unoccupied (inactive) since at least 1998 (range: 6–13 years). Last, 7 control sites (control) were established on grassland areas where prairie dogs were absent, but where soil type, topography, and vegetation were similar to colonies, and where there was no known history of cultivation.

One grid, consisting of 60 (1.35 ha; colony sites) or 100 (2.25 ha; control sites) Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida), was livetrapped on each of the 31 sites for 4 consecutive nights between 17 May and 5 August 2004. In an attempt to increase sampling effort on active colonies, three 2.25-ha (100 trap) grids were established on each of 4 active colonies in August 2004, for a total of 12 active colony grids. Grids on a given colony were usually >100 m apart. These grids and 6 of the control grids were trapped once for 4 consecutive nights between 24 August and 30 September 2004.

Traps were set at dusk, checked at dawn, and then reset for an additional 4–5 h to capture diurnal ground squirrels. All animals captured were weighed, identified by sex, age and reproductive status, and marked with a uniquely numbered aluminum ear tag (National Band and Tag Co., Newport, Kentucky). Blood, tissue, and flea samples were collected for future analyses. Research on live animals was approved by the Institutional Animal Care and Use Committee at California State University Fullerton, and was performed humanely following guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Habitat characteristics were recorded at 30 random points at each of the 31 original grids to determine the effects of prairie dogs on plant communities and habitat for other species. Vegetation height, shrub and burrow densities, and percent canopy cover of plant species in a 0.25-m^2 Daubenmire quadrat were recorded at each point. I used the mean of each variable for each site in subsequent data analyses, that is, sites were replicates. Percent cover data were arcsine-square-root transformed and other habitat variables were log-transformed before analysis. Thirteen transformed habitat variables (see Table 3) were included in a stepwise multiple regression to determine which of the habitat variables best explained abundance of the most common rodent species, total rodent abundance, and rodent species richness from the May–early August trapping. The alpha value for factors to enter and stay in the model was set at 0.10.

Patterns of rodent abundance and structural habitat characteristics were analyzed by analysis of variance (ANOVA) and multiple regression in SAS 9.0 (SAS Institute, Inc., Cary, North Carolina). Because population densities of rodents in shortgrass steppe are relatively low (< 4/ha—Stapp and Van Horne, in press), I used the number of individuals per 100 trap-nights as an index of relative abundance, which was then square-root transformed before analysis by analysis of variance (ANOVA) and multiple regression. The total number of trap-nights was adjusted by subtracting 0.5 trap-night for every trap that was sprung but empty. Multivariate analyses of rodent and plant communities were conducted by nonmetric

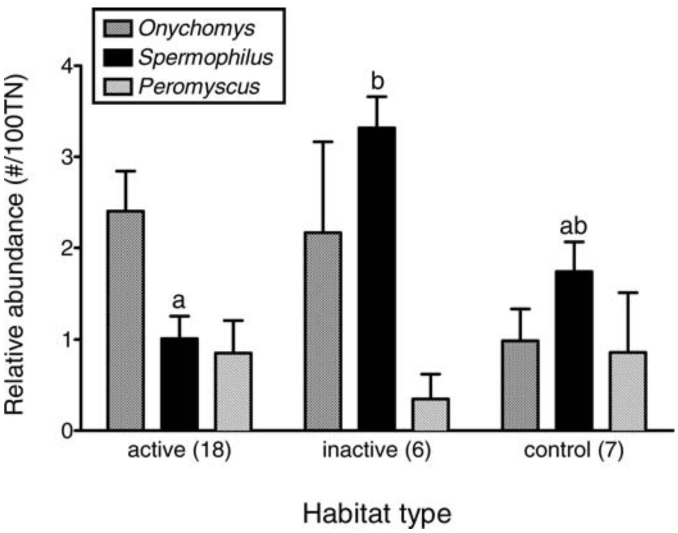

FIG. 1.—Relative abundance (mean ± *SE*) of northern grasshopper mice (*Onychomys*), 13-lined ground squirrels (*Spermophilus*), and deer mice (*Peromyscus*) in active and inactive prairie dog colonies and grassland sites without prairie dogs (controls). The number of sites sampled (May–August) is given in parentheses. For a given species, bars with the same letters were not significantly different from one another (ANOVA, Tukey multiple comparisons, $P > 0.05$).

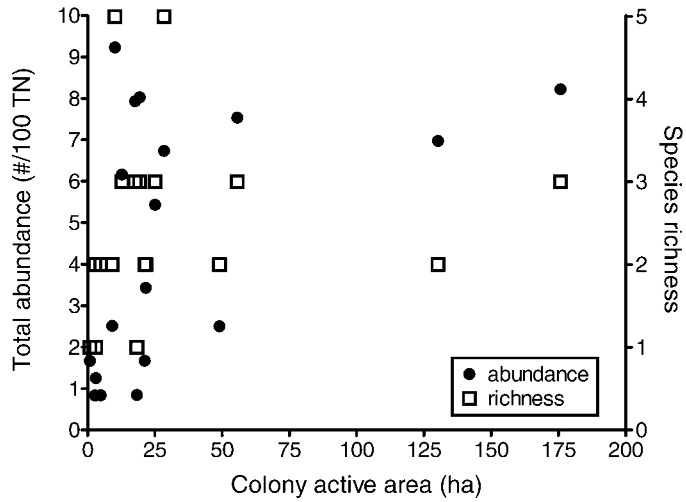

FIG. 2.—Relationships between colony active area (ha) in 2003 and total rodent abundance (filled circles) and species richness (open squares) on active prairie dog colonies ($n = 18$) in summer 2004.

multidimensional scaling (MDS) in PRIMER 5.0 (Clarke and Gorley 2001). MDS is an iterative, nonparametric ordination procedure that uses ranks of Bray–Curtis similarity coefficients to represent samples (here, sites) in 2-dimensional space, so that the distance between sites on a biplot is a good indicator of the similarity in species composition between them. The nonmetric MDS is produced by iteratively fitting nonparametric regressions of the distances between sites in 2-dimensional space on the similarity values. The final stress coefficient provides a measure of goodness-of-fit of the regression, with large stress values (>0.20) indicating difficulty in expressing the relationships among the sites in 2 dimensions. The SIMPER procedure was used to determine which rodent species contributed most to any observed differences between habitats. Data were transformed (4th root or log[y + 1]) before MDS analysis.

Comparisons of differences between multivariate representations of rodent communities and habitat characteristics among habitat types were analyzed using an analysis of similarity procedure (ANOSIM) in PRIMER 5.0. ANOSIM is a nonparametric permutation test conducted on the ranks of the similarity matrix among sites (Clarke and Gorley 2001). ANOSIM calculates a test statistic (R) that compares the rank similarities within and between habitat types. New values of R are then computed under multiple permutations of the replicate site labels. Significance values are calculated by comparing the observed value of R to the permutation distribution. If a global test of habitat differences was significant, pairs of habitat types were compared by repeating the test using only the ranks of similarity matrix from the 2 habitat types. The RELATE procedure was used to test and estimate the degree of concordance between similarity matrices for the rodent and plant community data (Clarke and Gorley 2001).

RESULTS

Northern grasshopper mice and 13-lined ground squirrels were the most common small mammals captured, comprising 40% and 34% of 401 total individuals, respectively, and occurring on 90% and 87%, respectively, of the 31 sites. The deer mouse, the third most abundant species, was captured on 45% (14) of the sites and comprised 16% of individuals captured. Although grasshopper mice tended to be more abundant on colonies collectively ($n = 24$) than on control sites ($n = 7$; $F = 2.97$, *d.f.* = 1, 29, $P = 0.096$), there were no significant differences among habitat types in the abundance of grasshopper mice ($F = 1.46$, *d.f.* = 2, 28, $P = 0.249$; Fig. 1) or any other nocturnal species ($P > 0.289$). Ground squirrels were least abundant on active colonies, and most abundant on inactive colonies and controls (ANOVA, $F = 9.52$, *d.f.* = 2, 28, $P < 0.001$; Fig. 1). Variation in the aboveground activity of squirrels between May and July may have confounded comparisons of abundance because a few sites were trapped in May, closer to the typical time of emergence of squirrels from hibernation (March—Flake 1974). Analysis of squirrel numbers only on sites trapped from 1 June to 5 August ($n = 26$) mirrored the results in Fig. 1, with squirrels most abundant on inactive colonies, least abundant on active colonies, and with control sites intermediate ($F = 8.54$, *d.f.* = 2, 23, $P = 0.002$). Combining across all species, rodent abundance did not differ among habitats ($F = 0.83$, *d.f.* = 2, 28, $P = 0.446$), regardless of whether all colony sites were pooled and compared to controls ($F = 0.37$, *d.f.* = 1, 29, $P = 0.803$). However, total rodent abundance in 2004 was related to the active area of the colony in fall 2003 in a nonlinear fashion (Fig. 2). Rodent abundance was lowest on the smallest colonies and tended to increase with colony area until approximately

30 ha, after which there was little change in rodent abundance with increasing colony size. However, even after the smallest active colonies (<10 ha; $n = 5$) were omitted, there was still no significant difference in total rodent abundance ($F = 0.72$, $d.f. = 2, 23$, $P = 0.498$) among colony types and controls. Total rodent abundance also did not differ between active and inactive colonies and controls when only the largest colonies (48–175 ha; $n = 4$) were included in the analysis ($F = 1.01$, $d.f. = 2, 14$, $P = 0.389$).

Species richness ranged from 1 to 6, but most of the 31 sites had only 2 species. Species other than the 3 most common ones were captured on only 10 of the 31 sites. Silky pocket mice (*Perognathus flavus*) were captured at 5 sites (3 controls, 1 active, and 1 inactive), hispid pocket mice (*Chaetodipus hispidus*) and western harvest mice (*Reithrodontomys megalotis*) were captured at 4 sites (2 controls and 2 active colonies each), and Ord's kangaroo rats (*Dipodomys ordii*) were captured at 3 sites (2 controls and 1 active). Harvest mice and hispid pocket mice were captured at different sites than kangaroo rats and silky pocket mice (each pair co-occurred on 3 sites). I also captured 1 prairie vole (*Microtus ochrogaster*) and 1 house mouse (*Mus musculus*). Rodent species richness was significantly higher on control sites (3.86 species ± 0.51 *SE*) than on active (2.50 ± 0.27 species) colonies, but was not statistically different from inactive colonies (Tukey's honestly significant difference; 2.50 ± 0.34 species; $F = 3.68$, $d.f. = 2, 28$, $P = 0.038$). As with total abundance, species richness in 2004 was also nonlinearly related to 2003 colony area (Fig. 2), but the highest richness values were from intermediate-sized colonies. Omitting the smallest active colonies (<10 ha; $n = 5$), which had the fewest species (1 or 2 species), species richness tended to be higher on controls, but not significantly different, than colony sites ($F = 2.58$, $d.f. = 2, 23$, $P = 0.098$). Considering only the largest active colonies (48–175 ha; $n = 4$), there again was a tendency for controls to have higher species richness than active and inactive colonies ($F = 3.50$, $d.f. = 2, 14$, $P = 0.059$).

Trapping on active colony and control grids in late August and September yielded similar results (Table 1), except that kangaroo rats and deer mice were captured more often on colony grids, and that species richness decreased on controls and was equivalent to that on active colonies. Numbers of most rodents, including ground squirrels, had declined by late summer, in part because squirrels began to disappear with the onset of hibernation; however, ground squirrels were significantly less abundant on active colonies than on control grids ($F = 5.34$, $d.f. = 1, 16$, $P = 0.034$). There were no significant differences in abundance of any other species or total rodent abundance between active colonies and controls ($P \geq 0.238$; Table 1). If the means of the 3 grids on each active colony are used in the analysis instead of the values from each grid, there are no significant differences in the abundance of any species, total abundance, or species richness ($P \geq 0.231$).

Rodent communities on inactive colonies tended to cluster together in multivariate analyses (Fig. 3a), but there were no significant differences among types of colonies or grassland sites (ANOSIM; $R = 0.049$, $P = 0.276$), in part because species richness across all sites was relatively low (10 species total). The moderate stress coefficient (0.17) indicated that the 2-dimensional plot adequately represented the higher dimensional relationships among the samples (Clarke and Gorley 2001). The abundance of ground squirrels and grasshopper mice contributed the most (26–44% and 31–35%, respectively) to pairwise dissimilarities between habitats (SIMPER analysis).

Table 1.—Mean (± *SE*) number of unique individuals per 100 trap-nights of each species captured, total rodent abundance, and species richness on 4 active prairie dog colonies (three 2.25-ha grids per colony) and 6 control grids in late August and September 2004. Values in parentheses are the number of grids (out of a total of 12 active colonies or 6 controls) in which each species was captured. The *P*-value is the result of ANOVA tests to compare differences in relative abundance between colonies and controls ($d.f. = 1, 16$). Additional species were captured on too few grids in late summer 2004 to warrant statistical analyses (silky pocket mouse: 2 active grids and 1 control; prairie vole: 1 control; plains harvest mouse [*Reithrodontomys montanus*]: 1 active grid and 1 control).

Species	Active colonies ($n = 12$)	Control sites ($n = 6$)	P
Northern grasshopper mouse	0.72 ± 0.20 (10)	0.50 ± 0.14 (5)	0.699
Deer mouse	0.48 ± 0.23 (7)	0.17 ± 0.12 (2)	0.321
Thirteen-lined ground squirrel	0.08 ± 0.04 (4)	0.51 ± 0.21 (4)	0.034
Ord's kangaroo rat	0.36 ± 0.13 (6)	0.13 ± 0.13 (1)	0.238
All species combined	1.77 ± 0.39	1.68 ± 0.49	0.898
Rodent species richness	2.50 ± 0.36	2.50 ± 0.72	0.817

Comparisons of percent cover of the most common plant species revealed few significant differences among habitat types (Table 2). Inactive colonies had significantly higher cover of lichens than did active colonies and controls ($F = 3.50$, $d.f. = 2, 28$, $P = 0.044$), and more *B. gracilis* and *Opuntia polyacantha* than active ones ($P < 0.05$), with control sites intermediate. Active colonies tended to have more *Salsola iberica* than inactive colonies and controls ($F = 2.94$, $d.f. = 2, 28$, $P = 0.070$). When analyzed on a species-wise basis, plant communities on inactive colonies tended to cluster together, but colonies and controls were not significantly different (ANOSIM, $R = 0.032$, $P = 0.346$). I repeated the MDS analysis after combining percent cover values into 6 functional groups (warm-season grasses, cool-season grasses, native forbs, exotics, cacti, and shrubs; based on the work of Hazlett [1998]), plus cover of litter and bare ground. This analysis revealed that functional group composition differed among habitats ($R = 0.160$, $P = 0.014$), with post hoc pairwise comparisons indicating that inactive colonies were significantly different than controls and active colonies ($P < 0.016$; Fig. 3b). Analyses of the percent similarity of plant functional groups among habitat types (SIMPER) indicated that the cover of warm-season grasses (23–31%), litter (19–28%), and bare ground (16–25%) were responsible for most of the dissimilarity in pairwise comparisons between habitats. Although there were no significant differences among habitats in multivariate analysis of rodent communities, patterns in the rodent

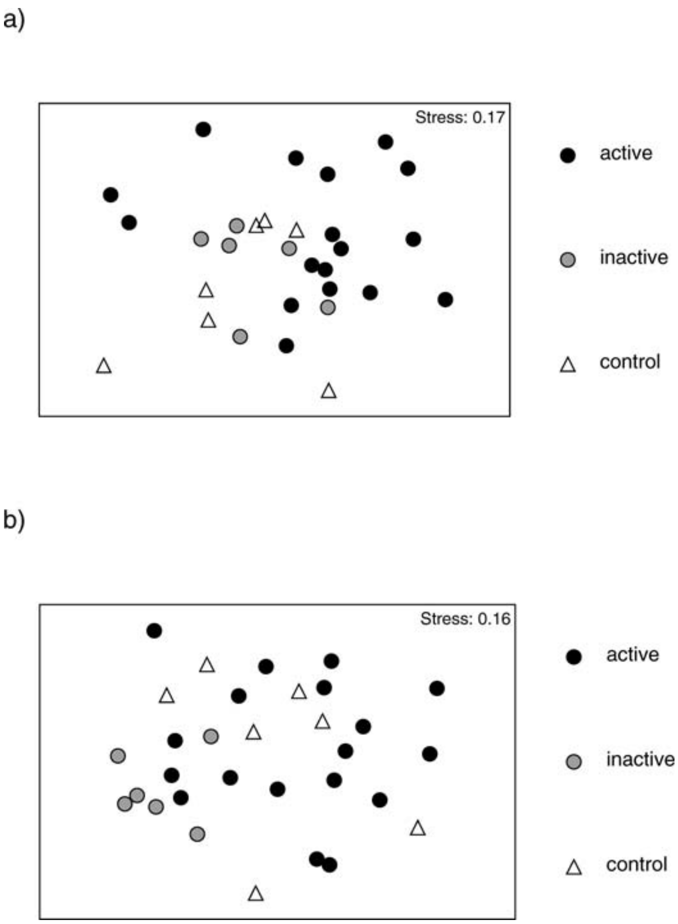

FIG. 3.—Nonmetric multidimensional scaling (MDS) plot showing relationships among a) rodent communities and b) plant communities as defined by functional groups (Table 3) in and out of prairie dog colonies in shortgrass steppe. MDS plots show the relative relationships among sites and, therefore, the axes have no units.

communities were significantly correlated with plant functional group composition (RELATE procedure comparing similarity matrices; Spearman correlation, $r = 0.144$, $P = 0.018$).

An ANOVA to examine habitat-related differences among functional groups revealed that heights of grasses and forbs were greatest on controls and lowest on active colonies (Table 3). Active colonies had the highest densities of prairie dog burrows, whereas inactive colonies had the most cacti and small burrows, primarily those of ground squirrels. Inactive colonies also tended to have more litter, less bare ground, lower plant species richness, and less cover of exotics (Table 3). Active colonies tended to have higher cover of native forbs.

Multiple regression analyses indicated that grasshopper mouse abundance was positively related to percent cover of forbs and bare ground and negatively related to percent cover of exotics and plant species richness (Table 4). Ground squirrel abundance was negatively related to density of prairie dog burrows and percent cover of exotics (Table 4). Deer mice were more abundant on sites with high cover of exotics and native forbs and low cover of cool season grasses. Combining all species, total abundance was positively related to cover of native forbs, and negatively related to density of prairie dog burrows (Table 4). Grass height and percent cover of bare ground were the best predictors of rodent species richness, mostly because kangaroo rats, pocket mice, and harvest mice tended to be captured on sites with taller grasses and forbs (Table 4; Fig. 4).

DISCUSSION

Patterns of rodent abundance in and out of colonies.—As in other areas of northern shortgrass steppe, northern grasshopper mice and 13-lined ground squirrels were the most abundant small mammals in and out of prairie dog colonies (Stapp and Van Horne, in press). Although grasshopper mice were more abundant, on average, in colonies than in grassland areas without prairie dogs, there were no consistent or significant differences in relative abundance among colony types and control sites. This result was somewhat unexpected because others (Agnew et al. 1986; Lomolino and Smith 2003; O'Meilia et al. 1982; but see Davidson et al. 1999) have reported higher numbers of grasshopper mice in colonies compared to areas without prairie dogs. In a separate study of rodent populations in 5 colonies and paired control plots conducted over a 2-year period (Stapp and Van Horne, in press), grasshopper mice also were found to be slightly more

TABLE 2.—Means (± *SE*) of percent cover of major plant species in and out of prairie dog colonies, based on measurements taken at 30 points at each site. Sample size (number of sites) is given in parentheses. Only plant species found on >20% of all 31 sites and comprising >1% mean cover on any habitat type were included. Different letters within a row denote significant pairwise differences (ANOVA with Tukey postcomparison tests; percentages were arcsine-square-root transformed before analysis).

Plant species	Habitat type (*n*)			*P*
	Active (18)	Inactive (6)	Control (7)	
Aristida purpurea	3.51 ± 1.20	0.69 ± 0.60	1.76 ± 0.73	0.208
Bouteloua gracilis	9.31 ± 3.20a	25.23 ± 2.54b	14.54 ± 3.57ab	0.009
Buchloe dactyloides	12.98 ± 3.06	6.14 ± 1.92	16.69 ± 7.78	0.683
Capsella bursa-pastoris[a]	1.52 ± 0.48	2.53 ± 0.58	3.24 ± 1.59	0.304
Opuntia polyacantha	1.07 ± 0.36a	4.04 ± 1.02b	1.64 ± 0.82ab	0.010
Pascopyron smithii	3.10 ± 1.04	0.52 ± 0.28	0.88 ± 0.49	0.158
Salsola iberica[a]	1.09 ± 0.43	0.01 ± 0.01	0.36 ± 0.30	0.070
Sphaeralcea coccinea	2.36 ± 0.44	1.97 ± 0.78	1.24 ± 0.49	0.347
Lichens	0.38 ± 0.18a	1.15 ± 0.34b	0.34 ± 0.34a	0.044

[a] Exotic species (Hazlett 1998).

Table 3.—Means (± *SE*) of habitat variables based on measurements taken at 30 points at each site. Sample size (number of sites) is given in parentheses. Different letters within a row denote significant pairwise differences (ANOVA, Tukey postcomparison tests).

Variable	Habitat type (*n*)			*P*
	Active (18)	Inactive (6)	Control (7)	
Grass height (cm)	5.25 ± 0.49a	5.96 ± 0.47ab	10.13 ± 1.90b	0.005
Forb height (cm)	5.12 ± 0.27a	6.31 ± 0.71ab	7.00 ± 0.92b	0.034
Prairie dog burrows (within 3-m radius)	0.31 ± 0.03a	0 ± 0b	0 ± 0b	0.001
Small burrows (within 1-m radius)	0.07 ± 0.02a	0.24 ± 0.08b	0.10 ± 0.03ab	0.007
Daubenmire quadrats				
Plant species richness (site total)	15.89 ± 1.08	11.50 ± 2.05	13.43 ± 2.13	0.074
Warm-season grasses (%)	25.99 ± 3.46	32.21 ± 1.67	35.80 ± 6.73	0.242
Cool-season grasses (%)	4.68 ± 1.18	3.20 ± 0.63	4.14 ± 1.57	0.958
Native forbs (%)	5.74 ± 1.12	2.34 ± 0.82	2.95 ± 0.88	0.083
Exotics (%)	2.31 ± 0.80	0.02 ± 0.01	4.82 ± 2.60	0.086
Cacti (%)	1.07 ± 0.36a	4.04 ± 1.02b	1.64 ± 0.82ab	0.010
Shrubs (%)	0.67 ± 0.22	0.39 ± 0.39	1.36 ± 0.60	0.180
Litter (%)	27.85 ± 2.86	37.96 ± 2.65	24.17 ± 3.29	0.070
Bare ground (%)	30.95 ± 3.16	18.69 ± 2.40	24.73 ± 2.75	0.070

abundant in colonies. Grasshopper mice were expected to be numerous in colonies because of this species' consistent use of burrows and mounds of pocket gophers and other animals (Stapp 1997). Independent of habitat type, grasshopper mice were most closely associated with cover of native forbs and bare ground, which tended to be highest on colony sites. Abundance of grasshopper mice also was positively correlated ($r = 0.46$) with the total number of prairie dog burrows on each grid (P. Stapp, in litt.). However, the lack of a significant difference among habitat types in the current study may simply reflect the fact that grasshopper mice are widespread but occur at relatively low densities, and that there is considerable local variability among sites in soil, vegetation, or prey availability that apparently masks any consistent effects of prairie dogs. Repeated sampling over multiple seasons and years may reveal a significant effect of prairie dogs on grasshopper mice.

I also found no significant differences in abundance of deer mice, which are commonly found in prairie dog colonies elsewhere, but primarily in mixed prairie or shrub-steppe vegetation (Agnew et al. 1986; Anderson and Williams 1997; Cully et al. 1997; Lechleitner et al. 1968). Deer mice are patchily distributed in shortgrass steppe, and are predictably captured only in areas with significant vegetative cover, including shrub-dominated areas, roadsides, or disturbed sites (Stapp and Van Horne, in press). Not surprisingly, the abundance of deer mice was positively related to forb cover and especially, the cover of exotic plant species. Sites where deer mice were captured in early–mid summer also tended to have other, less common rodent species; 6 of the 14 sites with deer mice had at least 1 other species besides grasshopper mice or ground squirrels, compared to only 3 of the 17 sites where deer mice were absent. This suggests that local habitat conditions on or near some study sites were favorable for deer mice and other cover-dependent species, independent of prairie dogs. Similarly, kangaroo rats were very abundant on 1 colony in spring 2004 and are occasionally captured in other colonies

Table 4.—Results of stepwise multiple regression to identify the habitat variables listed in Table 3 that best explained relative abundance and species richness of small mammals on 31 sites in and out of prairie dog colonies in northern Colorado. Abundance and richness were square-root transformed; habitat variables were arcsine-square-root or log transformed. Direction indicates the sign of the regression coefficient associated with a variable, indicating whether the relationship was positive or negative. The model R^2 is the cumulative coefficient of determination, so that the value associated with the final variable in the model represents the R^2 of the final model. Alpha-to-enter and alpha-to-stay were set at 0.10.

Species	Habitat variable	Direction	Model R^2	*F*	*P*
Northern grasshopper mouse	Native forbs (%)	+	0.334	14.52	0.001
	Exotics (%)	−	0.411	3.685	0.066
	Bare ground (%)	+	0.506	5.22	0.030
	Plant species richness	−	0.576	4.28	0.049
Thirteen-lined ground squirrel	Prairie dog burrow density	−	0.297	12.23	0.002
	Exotics (%)	−	0.380	3.74	0.063
Deer mouse	Exotics (%)	+	0.401	19.41	<0.0001
	Native forbs (%)	+	0.587	12.58	0.001
	Cool season grasses (%)	−	0.644	4.33	0.047
Total rodent abundance	Native forbs (%)	+	0.367	16.82	<0.001
	Prairie dog burrow density	−	0.443	3.83	0.061
Rodent species richness	Grass height	+	0.406	19.81	<0.0001
	Bare ground (%)	+	0.525	7.02	0.013

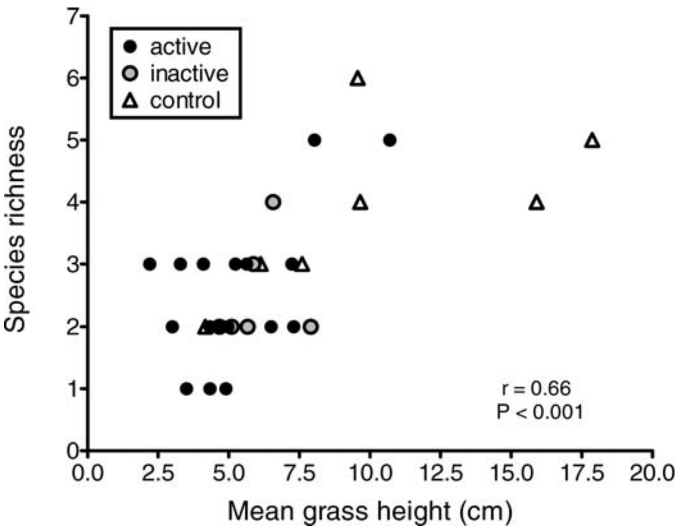

FIG. 4.—Species richness of rodents captured on 31 sites in and out of active and inactive prairie dog colonies as a function of mean grass height.

at other times (P. Stapp, in litt.), but they were relatively uncommon in the present study.

In contrast, ground squirrels were least abundant on active colonies, and their numbers were negatively related to the density of prairie dog burrows. Ground squirrels reached highest densities on inactive colonies, where vegetation cover was high and relatively homogeneous. Thirteen-lined ground squirrels are captured regularly in colonies, here and elsewhere (e.g., Cully et al. 1997), but the effect of prairie dogs on ground squirrel populations is not clear. O'Meilia et al. (1982) and Lomolino and Smith (2003) implied that 13-lined ground squirrels were more abundant in colonies, whereas others (Agnew et al. 1986; Stapp and Van Horne, in press) captured significantly fewer squirrels in colonies than in grassland sites. The mechanism by which prairie dogs might affect ground squirrels is not known; behavioral interactions between prairie dogs and other ground squirrels have not been studied. Alternately, the intensive grazing and disturbance caused by prairie dogs might indirectly reduce food availability (seeds and arthropods) or habitat for squirrels, or vertebrate predators attracted to colonies may incidentally prey on other species, including ground squirrels.

Combining all species, there was no significant difference in total rodent abundance between colony types and control sites. Total rodent abundance on active colonies was influenced by colony area, with small colonies having the fewest individuals and rodent abundance increasing with colony area until approximately 25 ha. This suggests that colonies must be of some minimal size to affect habitat quality or resources for other rodent populations, and that any benefits afforded to other rodents by prairie dogs are attained once colonies reach a certain size. However, there were no significant differences between active and inactive colonies and control sites when the smallest colonies were omitted, or when only the largest colonies were included in the analysis, and values of total abundance varied widely across the range of areas that are typical of most colonies on the PNG. In part, the lack of difference in total abundance reflects the contrasting effects of prairie dog colonies on grasshopper mice, which tend to be more abundant in colonies, compared to ground squirrels, which appear to be negatively affected by prairie dogs and therefore are more numerous in extinct colonies and on controls. Extremely large colonies (>100 ha) are rare on the PNG and are vulnerable to plague (Stapp et al. 2004), but it is reasonable to expect that total rodent abundance, or at least, that of grasshopper mice, might have been higher on colonies if I sampled more large colonies.

Effects of prairie dogs on plant and rodent communities.—As reported for other areas of shortgrass prairie (Barko et al. 2001; Klatt and Hein 1978; Winter et al. 2002), plant communities in colonies were not appreciably different from those in areas without prairie dogs, except that height of the vegetation was greater on control sites than on active colonies, and that active colonies tended to support more native forbs. The lack of strong contrast between plant communities of colonies and the surrounding grasslands is not surprising, given the long evolutionary history of grazing in this system (Milchunas et al. 1988). Colonies that had been inactive for $>$6 years were the most distinct, with high cover of *B. gracilis*, cactus, and lichens, and generally, less bare ground and fewer exotics (including *S. iberica*) and fewer plant species than other sites. Inactive colonies therefore appear to be transitional between the high levels of disturbance and herbivory in an active colony, and the relatively low levels of herbivory in grassland areas dominated by *B. gracilis*. Both *B. gracilis* and *Sporobolus cryptandrus*, another species that was uncommon on active colonies, are preferred food plants of prairie dogs (Bonham and Lerwick 1976).

Small-rodent communities on inactive colonies tended to be most similar to one another, primarily because of the relatively high numbers of ground squirrels captured on these sites. Only grasshopper mice and ground squirrels were captured on all but 1 inactive site. Overall, rodent communities were similar among types of sites, however, and differences among them could be usually attributed more to local, site-specific conditions than the presence of prairie dogs per se. Although abundance and richness are obviously correlated ($r = 0.59$, $P < 0.001$, $n = 31$), active colony area seemed to have less influence on species richness than on rodent abundance; for active colonies, the most species were found on intermediate-sized colonies, suggesting that the juxtaposition of smaller colonies and uncolonized grasslands may result in higher diversity. Indeed, among the 31 sites sampled in early–mid summer, rodent species richness was highest on grassland control sites, which was evident by the positive relationship between grass height and the presence of species that are relatively uncommon on shortgrass steppe. These include 3 heteromyids (Ord's kangaroo rat and silky and hispid pocket mice) and western harvest mice, which are typically found in areas with sandier soils, a higher diversity of seed-producing plants, or, in the case of harvest mice, taller vegetation (Stapp and Van Horne, in press). Several studies of the effects of prairie dogs on small mammal diversity have been completed recently (Agnew et al. 1986; Davidson et al. 1999; Lomolino and Smith 2003; O'Meilia et al. 1982), and only 1 (Ceballos et al. 1999) reported higher species richness in colonies than in similar grassland sites (richness on their 1 control site was intermediate between that of the 2 colonies they sampled). The close association between prairie dogs and several species of conservation concern (black-footed ferret [*Mustela nigripes*], burrowing owl [*Athene cunicularia*], mountain plover [*Charadrius montanus*], and ferruginous hawk [*Buteo regalis*]) is well established, and the burrowing and grazing activities of prairie dogs modify habitat for other animals, albeit in ways that differ among grasslands (Kotliar et al. 1999; Stapp 1998). However, my results, although limited to two 4-day–night sampling periods over a single year of study, corroborate those of other studies in that other than prairie dogs themselves, rodent communities in colonies did not consistently support more species than in similar areas of shortgrass steppe without prairie dogs. The high rodent abundance associated with both active and inactive colonies, combined with the high biomass represented by large numbers of prairie dogs on active colonies, nonetheless underscores the importance of prairie dog colonies as distinct areas of biological activity and importance that contribute to grassland diversity at the landscape scale.

Implications for plague.—Although there was no statistical difference in the abundance of grasshopper mice between colonies and grasslands, the abundance of this species and the relative scarcity of other species suggest that, if a small rodent is involved in the spread and maintenance of plague in prairie dog populations in shortgrass steppe, it is likely to be the grasshopper mouse. They are known to harbor a large diversity of fleas, including prairie dog fleas (Thomas 1988), and their extensive use of burrows and carnivorous habits (Stapp 1997) expose them to fleas and carcasses of dead prairie dogs, which may increase rate of transmission (Thomas et al. 1989). Moreover, their wide-ranging habits (Stapp 1999) may serve to spread the disease among coteries and between colonies. Importantly, laboratory challenges of grasshopper mice have demonstrated greater resistance to *Y. pestis* from a population in Colorado, where the disease is known to occur, than in an area of Oklahoma where plague had not been reported (Thomas et al. 1988). Although deer mice are often mentioned as probable reservoirs in other systems (Davis et al. 2002), including those of other species of prairie dogs (Cully et al. 1997; Lechleitner et al. 1968), the relative scarcity of deer mice in most areas of shortgrass steppe suggests that it may not be an important maintenance host here unless the disease persists off colonies in other habitats, as is the case for plague in areas of Europe and Asia (Gage and Kosoy 2005).

Acknowledgments

I thank C. Cannon, J. Holm, and A. Benson for their assistance in field, and M. Lindquist, S. Sprague, and D. Tripp for their invaluable advice and logistical support. The project was funded by grants from the National Science Foundation to M. Antolin, P. Stapp, C. Webb, and K. Gage (EID-0327052), and to the Shortgrass Steppe Long-Term Ecological Research Project (DEB-0217631). Additional support was provided by the Department of Biological Science and the Faculty Development Center at California State University, Fullerton. Comments from 3 anonymous reviewers improved the manuscript.

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Submitted 21 June 2005. Accepted 17 July 2006.

Associate Editor was Rodrigo A. Medellín.